REDBAND TROUT RESPONSE TO HYPOXIA IN A NATURAL ENVIRONMENT

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ABSTBACT.—Redband trout (Oncorhynchus mykiss gairdneri) were observed approximately every 2 weeks in an intermittent southwest Idaho stream between August and December 1991. Instantaneous daytime dissolved oxygen concentration and water temperature declined from 4.0 to <2 mg/L and 17 to 2°C, respectively, during this period. Redband trout declined from a maximum captured of 48 on 28 August to 1 on 8 November in one series of pools. As conditions approached hypoxia, trout exhibited little movement and positioned themselves in water just deep enough to cover their dorsal fin. High densities of speckled dace (Rhinichthys osculus) were also present in each pool until drying. The response of these fish to such extreme habitat conditions is probably a primary factor accounting for their distribution within arid landscapes.

Key words: Oncorhynchus mykiss gairdneri, redband trout, Rhinichthys osculus, oxygen tolerance, aquatic surface respiration, intermittent streams, desert fishes.

Headwater streams often become intermittent during summer (Williams 1987). Fish unable to migrate to perennial reaches are trapped in isolated pools where they may be subjected to lethal conditions. Observations of behavioral responses and survival of stream fishes in these conditions are few (Tramer 1977, Matthews et al. 1982, Mundahl 1990). Conditions associated with isolated pools in intermittent streams include lack of space and cover (Capone and Kushlan 1991), widely fluctuating and often lethal pH (Capone and Kushlan 1991), temperature (Huntsman 1942, 1946, Bailey 1955, John 1964, Matthews et al. 1982, Mundahl 1990), and dissolved oxygen (Tramer 1977). The ability of fish to survive harsh habitat conditions (sensu Matthews 1987) has been attributed to physiological (Matthews 1987) and behavioral adaptations (Kramer 1987).

Arid-land rainbow trout (Oncorhynchus mykiss) occur in southern Oregon, southwestern Idaho, and northern Nevada. Behnke (1992) believes these fish are a form of Columbia River redband trout (O. m. gairdneri) that have adapted to arid-land streams characterized by extremes in stream flow, temperature, and dissolved oxygen; little is known of their life history or ecology (Kunkel 1976, Behnke 1992). This paper describes the demise of

most and the survival of a few redband trout under low dissolved oxygen concentrations in an intermittent stream in southwest Idaho.

STUDY AREA

The study was conducted on Sinker Creek, a second-order tributary of the Snake River in southwestern Idaho, approximately 1 km from the confluence with the East Fork of Sinker Creek (T4S, R2W, Sec. 19, 20, Owhyee County, Idaho). Elevation of the study area is 1100 m. The geomorphology of the area is characterized by coarse alluvial fill interspersed with bedrock in a basalt canyon. Riparian areas are mostly unvegetated, except immediately adjacent to pools where willow (Salix sp.) clumps overhang the stream channel. Dewatered streambed areas are unvegetated. The watershed is subjected to summer livestock grazing.

During 1991, streams throughout south-western Idaho were flowing at far below normal levels (U.S. Geological Survey 1992). Sinker Creek upstream of the confluence with the East Fork of Sinker Creek was dry with the exception of a few isolated reaches. Data are presented from the largest wetted reach that consisted of five pools (A–E, sequentially, downstream) separated by shallow riffle areas along a 300-m reach.

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METHODS

Fish populations and habitat conditions were monitored approximately every 2 weeks between 14 August and 5 December 1991. Fish behavior was observed for 30-60 min prior to sampling. High-water clarity and limited pool area and depth facilitated direct observations, especially later in the study. Beginning 28 August, a Smith-Root batterypowered backpack electrofisher (Model 11A) was used to collect all redband trout in each pool. Total length and weight were recorded (weights were not taken prior to 24 October), and trout >100 mm were differentially fin clipped to identify fish from individual pools (there was a distinct size class break at 100 mm: trout <100 mm are herein referred to as small and trout > 100 mm as large).

During each visit water temperature and dissolved oxygen (DO, mg O_2/L) were measured with a YSI (Yellow Springs Instrument Company, Inc.) Model 57. Measurements were made between 1000 and 1430 h on all dates at several locations throughout each pool at surface, mid-depth, and bottom.

Pool surface area was determined as a rectangle by averaging several length and width measurements; depth was measured at the same locations as temperature and DO. Measurements continued until a pool dried or until 5 December when continuous flow returned to the stream. On 14 August 1991 pieces of plastic flagging were placed in the dry streambed between pools and weighted down with leaves so flow events between sampling dates could be detected; none were detected prior to 5 December.

RESULTS

On 14 August 1991 one redband trout was observed in pool B and three in pool D; numerous speckled dace (*Rhinichthys osculus*) were observed in all pools. Water temperature and DO ranged from 7°C and 1.5 mg/L, where water emerged from the substrate, to 28.5°C and 11.5 mg/L at the end of the wetted reach downstream of pool E.

On 28 August 48 redband trout were captured: I in pool A, 23 in pool B, 9 in pool C, 15 in pool D, and 0 in pool E. Pool areas ranged from 8 to 27 m². Water temperature and DO ranged from 16.8 to 18.5°C, and 1.7 to 4.6 mg/L, respectively, at the up- and

downstream ends of the wetted reach. Between 28 August and 11 October all pools and riffles went dry with the exception of pool D. No trout were found in any pool other than pool D after 28 August. Numerous (>100) speckled dace (mean length 25 mm) were present in each pool until drying.

Between 28 August and 5 December the volume and surface area of pool D decreased from 10.5 to 0.5 m³ and 27 to 4 m², respectively. Maximum pool depth decreased from 81 to 18 cm, and mean pool depth went from 56 to 13 cm. Dissolved oxygen decreased from 3.7 mg/L on 28 August to 1.6 mg/L on 1, 6, and 11 October, Between 24 October and 22 November, DO increased slightly to 2.0-3.0 mg/L. Water temperature dropped throughout the study period (Fig. 1) and was less than 10°C after 6 October. On all dates DO was slightly higher at the surface than at the bottom (mean difference = 0.2 mg/L). On 22 November a thin layer of ice covered half of pool D. On 5 December, when continuous flow returned to Sinker Creek, water temperature was 5°C and DO was 9.5 mg/L (Fig. 1).

Redband trout in pool D declined from a maximum of 33 captured on 20 September to I on 16 November (Fig. 1). The increase in trout captured between 28 August and 20 September was probably due to increased capture efficiency caused by a reduction in pool area and not from relocation of trout from other pools. No marked trout were captured in a pool different from the one in which they were originally captured. Recapture success was ca 50% in September and October and 100% in November. In November there was little space left in pool D for redband trout to hide, and the pool was more accessible to electrofishing.

On several occasions dead redband trout were found along the edge of pool D: one on 1 October, two on 11 October, and five on 8 November. No dead redband trout were recovered from any other pools. Dead redband trout had not been scavenged, and no sign of scavengers was apparent during any site visit. Of the missing redband trout, most were not accounted for, and those that were found were all >140 mm. Smaller trout may have been buried in the extensive decaying leaf material present in each pool. On 1 October two trout died and on 11 October one trout died as a result of electrofishing.

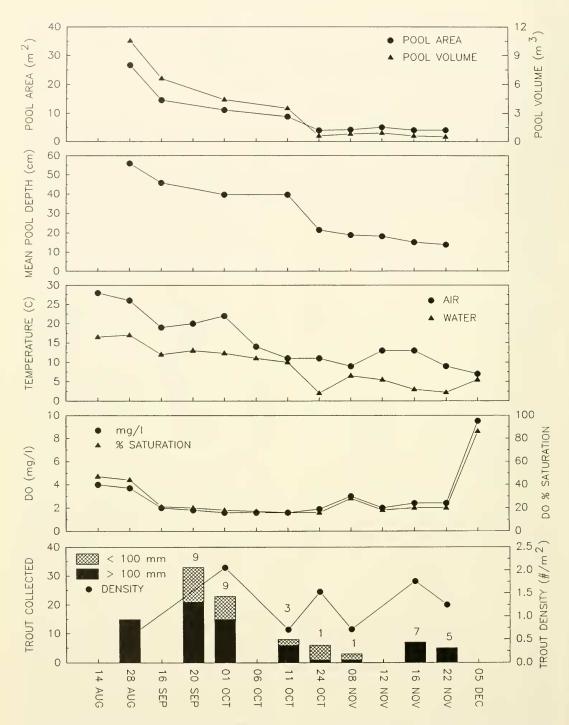


Fig. 1. Sinker Creek pool D volume, area, mean depth, air and water temperature, dissolved oxygen concentration and percent saturation, and trout numbers and densities (#/m²) between 14 August and 5 December 1991. Trout numbers and densities on 8, 16, and 22 November include trout transferred from the East Fork of Sinker Creek. n. are trout >100 mm (large). are trout <100 mm (small). There was a distinct size class break at 100 mm. Numbers above bars are recaptures of previously marked trout (>100 mm). Pool dimensions were not measured on 20 September, 6 October, and 5 December. Trout were not collected on 14 August, 16 September, 6 October, 12 November, and 5 December.

Prior to 24 October redband trout were observed swimming and surfacing throughout the pool. Approximately 60% of the pool could be effectively observed up to this date. Between 11 October and 24 October pool D shrank by 83% (Fig. 1), and the entire pool could now be observed. From this date on, redband trout were generally biding beneath small boulders in the middle of the pool or among the leaf debris along the shallow pool margins. Trout were rarely seen swimming around the pool. After being captured and returned to the pool, trout typically moved to shallow water along the shoreline and faced outward. While positioned along the pool edge, they occupied water just deep enough to cover their backs and "gulped" at the airwater interface. They remained in this position for at least 1 h. This post-capture behavior was probably a response to the stress of electrofishing. Speckled dace, whose densities were high throughout the study, showed no obvious change in behavior during the four months of observation.

On 8 November six large redband trout (145-222 mm) were captured by electrofishing and transferred from the perennial East Fork of Sinker Creek to pool D. Water temperature in the East Fork was 8.5°C and DO was 9.8 mg/L. In pool D water temperature was 6.5°C and DO was 3.0 mg/L. This transfer took ca 15 min. Immediately upon being placed in pool D, the redband trout moved to shallow margins of the pool and began "gulping" at the air-water interface. Over the next hour they remained along the edge of the pool facing outward with their dorsal fin just breaking the water surface. Opercular movements remained rapid during this time. The one original pool D large redband trout remained under a boulder in the middle of the pool and did not interact with the transplanted redband trout; the two remaining small trout were not observed.

On 12 November water temperature was 5.5°C and DO was 2.0 in pool D. Because the electrofishing unit was not functional, no redband trout were captured, but several were observed along the pool margins facing outward. On 16 November seven large redband trout were collected (one original pool D trout and the six East Fork redband trout). The two remaining small redband trout could not be

found. The six transplanted East Fork redband trout had all lost weight (1-8 g) since being transferred 8 days earlier; the accuracy of the scale was ca ±1 g. On 22 November three of the transplanted redband trout maintained the same weight as on 16 November, one lost 1 g, and two could not be found. The weight of the original pool D redband trout declined from 66 g on 11 and 24 October to 63 g on 8 November, 62 g on 16 November, and 60 g on 22 November.

DISCUSSION

One of 48 redband trout survived at least 114 days in DO <4 mg/L, and 4 redband trout transplanted from the perennial, high DO (9.8 mg/L) East Fork of Sinker Creek survived 43 days at DO <2.5 mg/L. Water temperature declined from 17 to 2°C during this period. Additional survival would probably have occurred if not for repeated electrofishing. The ability of arid-land redband trout to withstand harsh habitat conditions has been suggested by Wishard et al. (1984) and Behnke (1992). Behnke (1992) reported fishing for and catching arid-land redband trout in intermittent stagnant pools in Oregon. There are a few studies on water temperature tolerance of native western trout species (e.g., Lee and Rinne 1980), but no field observations have been previously made of native trout responses to low DO.

Effects of low DO on rainbow trout were summarized by Davis (1975). Negative effects of low DO first become apparent at 5-6 mg/L (Davis 1975). Responses of adult rainbow trout to DO <5 mg/L or <50% saturation include elevated breathing amplitude and buccal pressure (Hughes and Saunders 1970), reduced heart rate (Randall and Smith 1967), reduction in swimming speeds (Kutty 1968), and reduced capacity for anaerobic metabo-

lism (Kutty 1968).

A possible explanation for the survival of redband trout in this study might be that a seep with higher DO was entering this pool. We looked for such a source by measuring temperature and DO throughout the pool on each sampling date and by digging shallow groundwater wells into the streambed on 8 November. There was little variation in temperature and DO within pools for any date. Groundwater temperature was 2.5°C and DO

was 1 mg/L. Groundwater typically contains little or no dissolved oxygen (Hem 1985).

Probable factors contributing to fish survival included a long acclimation period (Shepard 1955, Davis 1975), especially when compared to laboratory studies, sedentary behavior (Davis 1975), declining air and water temperatures as the study progressed (Fig. 1), and lack of water velocity in either pool so that energy expenditures would have been minimal (Davis 1975). Sinker Creek probably became intermittent in May or June, after snowmelt runoff. Fish unable to escape downstream to the perennial East Fork of Sinker Creek had many weeks to become acclimated to the gradually deteriorating conditions.

Increased acclimation improves trout survival in low DO. Shepard (1955) showed that with sufficient acclimation time lethal DO levels for brook trout (Salvelinus fontinalis) larvae could be reduced to 1.05 mg/L at 8°C. Complete survival of larvae was achieved at the approximate acclimation rate of 70 h per each 1.0 mg/L decrease in O_2 at 9°C; fish in Sinker Creek probably had a more gradual aeclimation.

In the laboratory most fish species tend to move away from low DO areas and occupy higher locations in the water column (Kramer 1987), where DO is generally higher due to diffusion at the air-water interface. Early in the study redband trout were frequently seen swimming near the surface. As pool D shrank, most trout were observed in shallow water along the edge of the pool. Tramer (1977) observed Johnny darters (Etheostoma nigrum) lined up around pool margins with their heads facing outward in an oxygen-depleted pool. This position would provide easier access to the surface film where diffusion maintains higher levels of dissolved oxygen (Lewis 1970). The use of the surface film by fish is a response to low dissolved oxygen levels and is known as aquatic surface respiration (ASR, Lewis 1970). The ability to perform ASR is common among fishes living in hypoxia-prone waters (Kramer 1983), but it has not been reported for salmonids.

Shepard's (1955) observations of trout immediately surfacing upon the introduction of oxygen-deficient water to their tanks is the only evidence we could locate of salmonids performing ASR-type behavior. Gee et al. (1978) subjected rainbow trout, arctic char

(Salvelinus alpinus), and lake whitefish (Coregonus clupeaformis) to progressive hypoxia, and none exhibited ASR behavior. They felt salmonids might not have evolved this behavior because they typically occupy well-oxygenated waters. Arid-land redband trout may be an exception (Behnke 1992).

A major factor enhancing redband trout survival was that as the pool shrank, the proportion of groundwater flow to surface water flow increased and air temperatures declined. Increased influence of groundwater and lower air temperatures reduced water temperatures, diel fluctuations in dissolved oxygen, and fish metabolic rates. Tramer (1977) found that fish mortality in isolated pools was highest during periods of maximum water temperature and diel DO fluctuation. Whitmore et al. (1960) observed juvenile chinook salmon (O. tshawytscha) strongly avoiding low DO (1.5-4.5 mg/L) areas in the summer when water temperatures were high but not in the autumn when water temperatures were cool-

The ability of transplanted East Fork redband trout to survive in pool D was especially surprising. We initially expected that with their lack of acclimation to low DO levels, pool D would be lethal (Davis 1975). Although they appeared stressed initially, four of the six trout survived 43 days until perennial flow returned. Immediately upon being placed in pool D, these fish appeared to perform ASR. On subsequent visits they were usually seen lying along the pool margin partially covered by fallen leaves. Their breathing rate appeared relaxed and was much slower than when they were introduced into pool D.

Lowe et al. (1967) found greater survival of smaller-bodied native Arizona fishes in low oxygen concentrations than larger-bodied fishes. Shepard (1955), however, found that larger trout (12 g) tended to live longer at lethal DO levels than larval fish (1 g). In this study a large (146 mm, 60 g) redband trout outlived all small (<100 mm) redband trout in pool D, while just downstream in another pool of similar size eight small and no large redband trout survived (Vinson unpublished data). Speckled dace survived in high numbers in all pools until drying.

Although most of the redband trout died during our study, their ability to survive even a short time in these extreme habitat conditions. including our repeated electrofishing, which we feel may have been a source of delayed mortality, is noteworthy. The use of surface film water (ASR-type behavior) may be a strategy these fish use to survive periods of hypoxia in their harsh desert stream environment. Future study is needed to better describe the physiological tolerances of this desert fish species.

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